A Dynamic Programming Approach to the Breeding Seasons of Birds

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The time of breeding in birds has long been of general interest to biologists. Charles Darwin (1874, pp. 215-218) collected together data showing that more vigorous females breed earlier. He developed the implications of this observation for his theory of sexual selection, and Fisher (1958, pp. 153-155) provided a numerical elaboration of this idea. Price, Kirkpatrick and Arnold (1988) recently carried this line of theoretical research forward by exploring how directional selection can appear to act on breeding date without actually causing a shift in the trait's distribution. This interest in breeding time has largely concentrated on the consequences of individual breeding times relative to a population-level distribution, rather than the ecological factors affecting the value of the population's mean.

This latter topic has been pursued by ornithologists asking questions about how and why a breeding season occurs when it does. Baker (1938) cast this question in general terms, introducing along the way the now-venerable distinction between proximate and ultimate causes of organisms' features. Since then, studies of the proximate mechanisms of breeding-season determination have contributed an enormous amount to our understanding of the endocrine and reproductive systems of birds (e.g., Murton and Westwood 1977), and we have learned a great deal more about the ultimate factors that appear to have shaped the timing of breeding seasons (e.g., Perrins 1970, 1985). The environmental factors to which breeding seasons are most often thought to have evolved are food supply and safety from predators (Perrins 1985), but several other features of the environment, i.e. daylength and temperature, seem likely to be important.

To weigh the potential importance of daylength, temperature, food supply and predation, we developed a dynamic optimization model for the timing of breeding of birds in temperate environments. We here describe the model and its results and discuss their relevance to our understanding of breeding seasons.

THE MODEL

Our model uses the standard techniques of dynamic optimization (Mengel and Clark 1988). To approach the problem of breeding-season determination with dynamic programming, we

assume that the fitness of a parent bird is a function of its own condition (= "state") and that of its offspring on the day that the offspring fledge. We then assume that the changes in state of the parent and its offspring can be defined as a function of the activities of the parent (e.g., how much time the parent spends foraging for itself and its offspring). The optimization then consists of working backward in time through the year from the point of fledging of the offspring to some point in advance of the beginning of the breeding season, keeping track of the optimal actions of the parent and the fitness of the parent pursuing the optimal trajectory through time and state-space. The choice of the optimal time of breeding is accomplished by comparing the fitnesses of the optimally behaving parents that fledge their offspring on different days relative to an environmentally dictated cycle in daylength, temperature and food density.

In the following paragraphs, we describe the model in greater detail, first compiling all the notation that we use, then describing the model's structure in detail, and finally giving our rationale for the choice of parameter values used in our runs of the model.

NOTATION

The following notation is used:

y is the temperature of the environment.

t is the biological time. The terminal time, that is the time of fledging is $t = 360$. When $t = 300$ it should be taken to mean 60 days before fledging. (For convenience, we operate on a 360-day year.)

a is the age of the chick.

w and z are the states of the parent and brood, respectively. We assume that state in the form of weight can be converted to energy according to the translation of 1 g equal to 9 kcal. Although we treat weight and state interchangeably, the program actually computes everything in terms of kcal.

n is the number of chicks.

The subscript n in w, z, and n means "new" i.e., w_n, z_n is the weight of parent or chicks the following day and n_n the new number of chicks.

F is the fitness function. It depends on w, z, n and t.

x_1 and x_2 is the time that the bird spends foraging for itself and its chicks, respectively. Time is measured in hours.

x_{max} is the maximum number of hours that the bird can forage per day.

q is the probability of not being attacked per foraging hour.

e is the probability of escaping once attacked.

c_1 is the metabolic cost of the parent per day.

c_2 is the metabolic cost of an individual chick per day.

g is the energetic cost of foraging per hour.

r is the feeding rate per hour. This does not include decrements for the foraging cost, but it includes decrements for every other energetic cost (assimilation of food, etc.).

s_{min} = minimum chick state.

s_{max} = maximum chick state.

THE MODEL

The model can be described by the equation:

$$F(w,z,n,t) = \sum_{y} max \{ F(w_n,z_n,n_n,t+1) [q^{x_1+x_2} + (1-q^{x_1+x_2}) e(w)]\} P(y) \qquad (1)$$

The maximum is taken over the possible values of x_1, x_2 and n_n. We must have $0 \leq x_1 + x_2 \leq x_{max}$ and $n_n \leq n$. The summation is over all possible values of temperature (y).

The rationale for the equation is as follows: On a particular day the temperature is y with probability $P(y)$. Given the value of temperature, the program chooses x_1, x_2 and n_n so that it maximizes fitness conditional on the value of y. The fitness on day t is, by the law of conditional expected value, the sum over the possible values of y of the conditional maximized fitnesses on day $t+1$ times the probability that the temperature is equal to y. The restrictions $0 \leq x_1 + x_2 \leq x_{max}$ and $n_n \leq n$ are necessary because the time that the bird forages cannot exceed a certain

maximum and the new brood size cannot be larger than the old one. (Special attention is needed on the hatching day.)

For a given pair of x_1 and x_2, the bird's probability of not being attacked during the whole day is $q^{x_1+x_2}$ and the probability of being attacked and escaping is $(1-q^{x_1+x_2})e(w)$. Thus the bird will survive its predators with probability $q^{x_1+x_2} + (1-q^{x_1+x_2})e(w)$. If it survives, the bird's new state (w_n) will be:

$$w_n = w + r x_1 - g(x_1 + x_2) - c_1 \tag{2}$$

truncated at some w_{min} and w_{max}. The value of w_{min} is such that if $w \leq w_{min}$ the bird starves, and the fitness afterwards will be equal to zero. We do not allow $w_n > w_{max}$.

The new weight of the brood is:

$$z_n = \frac{z}{n} n_n + r x_2 - n_n c_2 . \tag{3}$$

We also truncate z_n at some minimum and maximum values. We first specify s_{min} and s_{max} which represent the minimum and maximum weight that an individual chick can have. We do not allow z_n to be greater than $n_n s_{max}$ or less than $n_n s_{min}$.

Equations (2) and (3) describe the energetic balance of the bird and its chicks for day t. The bird starts the day with state w and its energy intake is $r x_1$. Its energy expenditure is its foraging cost, which is proportional to its foraging hours, and its metabolic cost, which may depend on environmental conditions but does not depend on x_1 and x_2. At the end of the day the new weight will be the right hand side of (2).

The brood, in the beginning of the day, has total weight z which is assumed to be equally distributed among the n chicks. If the parent decides to feed only n_n chicks and let the rest of them die, then the total brood weight that will be carried to the next day is $\frac{z}{n} n_n$, the number of surviving chicks times their individual weight. Note that $\frac{z}{n} n_n \leq z$ because if some chicks die, their weight is lost. The parent's energy harvest during the day is the number of hours the parent forages for the chicks multiplied by the feeding rate per hour. We assume that the parent distributes the food

equally among its chicks and that the effect of energy intake on the increase in brood weight does not depend on the number of chicks. Brood energy expenditure is proportional to the number of chicks; each chick requires c_2 kcals per day. Growth and maintenance metabolic cost are both included in c_2.

During the non-breeding season, equation (1) still describes the model but requires some adjustments. F is maximized over all possible values of x_1, i.e., x_2 always takes the value zero. We force $n_n = n$ and $z_n = z$ and n and z now have different meanings. n is the number of eggs that the bird will lay in the beginning of the breeding season. z depends on n but it does not change during the non-breeding season. It stays equal to the weight of an egg times the number of eggs to be laid. In other words n and z represent "n chicks that will be and that will weigh z on the day of hatching".

For the last day, that is when $t = 360$, the fitness function is given by:

$$F(w,z,n,t) = I_{(w>w_{min})} + \alpha\, n\, \frac{\frac{z}{n} - s_{min}}{s_{max} - s_{min}} \tag{4}$$

$I_{(w > w_{min})}$ is the contribution of the parent to the terminal fitness function. It is defined to be equal to 1 if $w > w_{min}$ and 0 otherwise. α is a coefficient that represents the fitness value of one chick when fledging, relative to the parent. It can be thought of as the probability of survival to breeding for a chick having the maximum weight times its relatedness to the parent. When the brood has the maximum possible weight, then:

$$\frac{\frac{z}{n} - s_{min}}{s_{max} - s_{min}} = 1, \tag{5}$$

and the contribution of the chicks to the terminal fitness is αn. On the other hand, if the brood is starving:

$$\frac{\frac{z}{n} - s_{min}}{s_{max} - s_{min}} = 0 , \qquad (6)$$

and the terminal fitness is simply $I_{(w>w_{min})}$. For intermediate values of z we consider the possibility of survival to decrease linearly in weight. The quantity:

$$\alpha \frac{\frac{z}{n} - s_{min}}{s_{max} - s_{min}}$$

represents the relative contribution of a chick weighing $\frac{z}{n}$.

ASSUMPTIONS ABOUT THE PARAMETERS

For parameter values, we chose the Black-capped Chickadee (Parus atricapillus) nesting in the vicinity of Ithaca, NY, as a guide upon which our decisions would be loosely based.

(i) State of the parent (w)

If we consider the range of possible weights of a bird to be ± 20% of its average weight, for a 10 g bird this would be 2 g. Translating into units of energy by assuming that 1 g of weight is equivalent to 9 kcals, this translates to 18 kcals or a range of 36 kcals. Thus w_{min} = *72* kcal, w_{max} = *108* kcal.

(ii) State of the brood (z)

When a chick hatches, we assume it weighs 1.3 g ± 20%. We assume that it takes 3 weeks to fledge and that the increase in minimum and maximum weight as a function of age has a logistic form. Asymptotically, the two logistic curves will approach 8 g and 12 g respectively. The numbers that we used were:

$$s_{min} = \frac{8}{1+6.69e^{-0.230a}} \qquad (7)$$

and

$$s_{max} = \frac{12}{1+6.69e^{-0.252a}} \qquad (8)$$

(iii) Maximum foraging time per day (x_{max})

Daylength is assumed to vary as at Ithaca, NY (Fig. 1a), and the available hours for foraging per day is reduced by 20% during the five-day nest-building period and by 75% during the 10-day incubation period.

(iv) Temperature (y)

For a particular calendar day, the mean temperature is taken from means at Ithaca, NY (Fig. 1b), and the distribution of temperatures around this mean is a discretized normal random variable with standard deviation of ± 7.5° C.

(v) Metabolic cost for the parent (c_1)

We used Existence Metabolism (Kendeigh et al. 1977), since we do not include the foraging energetic cost or any other cost associated with reproductive activities. We assumed, after Kendeigh et al. (1977, p. 377), a functional relation with temperature of:

$$c_1 = 16.2 - 0.25y\,. \tag{9}$$

At the time of laying eggs we add an additional cost. Assuming that the energetic cost of an egg is 40% of the Basal Metabolic Rate (Ricklefs 1974), and that BMR for chickadees is 5.2 kcal/day (Kendeigh et al. 1977, p. 369) we used a value of 2 kcal/egg.

(vi) Energetic cost of foraging (g)

To calculate the energetic cost of foraging we multiplied BMR by a factor of 3.5 (Yom-Tov and Hilborn 1981, p. 236), yielding a cost of 0.75 kcal/hour.

(vii) Metabolic cost for the chicks (c_2)

This includes energy used for maintenance and growth and thus is slightly different than c_1. We used Kendeigh et al.'s (1977, p. 185) Daily Energy Budget for chicks, which includes locomotion and specific dynamic action. We assumed it to be independent of temperature because the parents are regulating the temperature of the young through brooding. The equation gives:

$$c_2 = 1.724\, s_a^{\,0.9} \tag{10}$$

where s_a is an average weight that the chick should have as a function of age. The functional form of s_a is analogous to (7) and (8), that is, it is logistic and starts at $s_a = 1.3$ when $a = 0$ and asymptotically tends to 10 g, the average weight of an adult. s_a is given by:

$$s_a = \frac{10}{1 + 6.69e^{-0.242a}} . \tag{11}$$

Substituting (11) in (10) we get c_2 as a function of age. The equation is:

$$c_2 = \frac{13.694}{(1 + 6.69 \exp(-0.242a))^{0.9}} \tag{12}$$

(viii) Food supply (r)

Food supply represents the maximum kcals that the bird is capable of gathering per hour. Food supply was assumed to be a random variable with mean $\bar{r}$ depending on time of year (Fig. 1c) and deviation from this mean dependent on temperature. If the temperature takes its minimum value, so does the food supply, and similarly when the temperature increases to its maximum, the food supply attains its maximum, as well.

Food supply varies between a minimum of 2.5 kcal/hour and a maximum of 10, and on a given day its standard deviation (sd_r) is determined by $sd_r = 0.1\,\bar{r} + 0.5$.

(ix) Number of chicks (n)

We start with clutch sizes between 0 and 11 eggs, and the brood size that is raised can be reduced below this by the activity of the parent.

(x) Probability of not being attacked per foraging hour (q)

We used the value $q = 0.999$, on the grounds that it seems reasonable that a bird foraging for, say, 2400 hours (i.e., about a year of foraging time) would have about a 10% probability of not encountering a predator at all.

(xi) Probability of escaping when attacked (e)

We assumed this is a function only of weight and that very weak and very fat birds cannot escape, i.e., $e(w_{min}) = e(w_{max}) = 0$. The form of $e(w)$ is assumed to be quadratic with maximum equal to 0.75, which occurs when $w = (w_{max} + w_{min})/2$.

RESULTS

Fitness increases with number of offspring in all our experimental runs, and in virtually all, this increase plateaus at 8 or 9 offspring (Fig. 2). This plateau results because parents can never raise larger than these numbers of offspring, and the optimal policy is always to let some offspring die very early in their development until a manageable number of offspring is reached.

For a given brood size, the optimal date of breeding can be compared for the two different food situations in our computer runs. For the birds experiencing an early food peak (henceforth the "E birds"), with 9 offspring the optimal date of breeding has chicks fledging on 10 June, 10 days after the food peak at the end of May (Fig. 3a). By contrast, the optimal date of breeding for the birds experiencing a late food peak (henceforth the "L birds") has them fledging their chicks only four days after the peak in food density (Fig. 3b). The total length of the nesting cycle is 45 days in both these groups, i.e., 5 days for nest-building, 9 days for laying 9 eggs, 10 days for incubating and 21 days for chick care. The distribution of the food supply also has an identical shape; the only thing that has been changed is the phase relationship of the food supply cycle with those of daylength and temperature (Fig. 3).

In considering the effect of variation in clutch size and parental weight on fitness and optimal date of breeding we find that, in both groups, variation in parental weight affects fitness extremely little and optimal date of breeding not at all (Fig. 4). Number of offspring has a considerable effect on fitness and an interesting effect on optimal date of breeding (Fig. 5), with the optimal date of breeding decreasing as clutch size is reduced. It must be kept in mind that this model is not a model of clutch or brood size optimization; the number of offspring is treated as a given parameter here, not as one of the factors optimized by the parent, and the only departure from the given number of offspring is that broods are allowed to be reduced by starvation.

So far, in determining the optimal dates of breeding, we have been comparing the fitnesses on a given calendar date of birds with different dates of fledging their young. If instead, we compare birds' fitnesses on a day a given constant number of days in advance of their fledging dates (Fig. 6), we obtain an estimate of optimal breeding date that is independent of the number of days still to be survived before breeding. Using this measure, the effect of offspring number on optimal breeding date is opposite to that observed on a calendar-date-basis.

DISCUSSION

The relatively earlier nesting by the L birds (Fig. 3b) as compared to the E birds (Fig. 3a) could be explained by a decline in daylength and temperature late in their nesting cycle selecting for earlier breeding. Alternatively, depressed daylengths and temperatures early in the nesting cycles of the E birds could be selecting for later breeding by them. Of these two possibilities, the latter seems most applicable, since the L birds would sacrifice very little in terms of daylength and even gain a bit more in terms of temperature if they shifted their breeding dates later (Fig. 3b). However, if the E birds shifted their breeding date earlier, they would lose both in temperature and in daylength (Fig. 3a).

Perhaps the most striking feature of the optimal timing of breeding in both the E and L groups is that the nesting cycle is not more evenly distributed to either side of the peak in food abundance. Drawings in Perrins (1970, p. 244) epitomize what we suspect would be the common a priori expectation for an optimal time of breeding: that it should be placed so as to maximize the net total amount of food available to the foraging parent. Why then do birds of both groups place their breeding seasons so far to the left of the food density distribution? One potential reason why this might occur in nature would be that there is considerable post-fledging parental care, and the parents are selected to breed earlier to allow for high food densities when they are feeding fledglings. This explanation cannot apply to the birds in our model environment. The chicks are assumed to be independent at fledging, and parents cannot gain any fitness by expending any parental care on them after they have fledged.

Another possibility to explain this shifting of the breeding season in advance of the peak in food availability is that the food requirements of the offspring are so extreme in the latter portion of the nesting cycle that the parents are selected to place the time of peak demand at the time of greatest food abundance. For example, the assumed daily metabolic demand of a single offspring at 20 days is approximately 13 kcal and only 5 kcal at 5 days of age (equation 12). These costs compare with parental spring metabolic demands of about 12.5 kcal (equation 9, Fig. 1b). Thus a brood of 9 chicks at 20 days of age, with a total daily demand of 117 kcal, can be a strong factor selecting for breeding when food is most available.

A great deal of the early shift can be explained by this coordination of the period of maximal chick demand with the food peak. A third explanation is required, however, to fully account for the model results. In attempting to explain the advantage of early breeding to males, Fisher (1958, p. 155) pointed out that "the death rates of animals are often surprisingly high, and a death rate of only one percent per week would give a considerable advantage to the earlier males." This effect is acting in our runs, since the birds are being selected to breed earlier by the simple fact that they may not live long enough to breed at an otherwise more favorable time.

Evidence for this view comes from the effects of clutch size on optimal breeding date (Fig. 5). As the physiological/ecological requirements of raising young (i.e., clutch size) decrease (recall that the parents are given their clutch sizes, they did not optimize them), the optimal time of breeding decreases. This suggests to us that the parents are choosing later breeding dates only in the presence of strong selection to breed later to feed a larger brood.

Further evidence comes from consideration of optimal breeding dates with "the time to go effect" removed (Fig. 6). When the fitnesses of all birds being compared are measured the same number of days in advance of breeding, then birds with smaller broods do better by breeding later, i.e., they shift their breeding cycle toward a more symmetric placement around the peak of the food distribution. Parents of the larger broods are still selected to place their breeding cycles in advance of the food peak, thus coordinating their maximal chick demands with the food peak.

Both these lines of evidence suggest that parents are breeding earlier than would otherwise be expected in response to the finite probability that they might die before or during a later breeding attempt.

This perspective on the optimization of breeding date emerges naturally from a dynamic programming approach since, by working back through time, it automatically accounts for the increasing death probability as the time of breeding is delayed. This result would not have been as apparent in a static optimization approach. More importantly, this result suggests that the phenomenon of non-zero death probabilities in nature may provide a source of directional selection on breeding dates that is largely independent of the ecological variations of individual environments and species. As such, it may be the most fundamental driving force behind the advantage of breeding early and the sexual selection that naturally follows.

SUMMARY

We here report the results of a dynamic programming model of the breeding season of a bird, patterned after the Black-capped Chickadee (Parus atricapillus) nesting near Ithaca, New York. Optimal breeding seasons fall largely before the peak in food distribution, and this shift appears to be because peak metabolic demands of the brood are coordinated with the peak in food density and because finite adult mortality rate selects for earlier breeding than would otherwise be favored.

ACKNOWLEDGEMENTS

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Figure 1. The cycles of environmental variables used in the timing of breeding model. a) Day length in minutes at Ithaca, New York, as a function of Julian date. For convenience, the year was truncated to 360 days, and the day length at day 360 is the same as for that on day 0. b) Temperature in °C at Ithaca, New York, versus Julian date, truncated as in a). c) Food supply in kcal/hr of foraging available to forest birds at Ithaca, New York, as a function of Julian date. For assumptions made in constructing this graph see text. This graph represents the cycle in food availability for the E group of birds discussed in text. Food availability for the L group is identical in shape, with every point shifted 30 days later. d) All cycles of environmental variables superimposed on a common vertical scaling of the proportion of their respective annual maxima.

Figure 2. Fitness as a function of brood size. This figure is for a parent with a weight of 10 g, with fitness measured on March 25 and with a breeding season ahead that will have chicks fledging on May 25. Curves of the same shape were obtained for virtually all combinations of variable values.

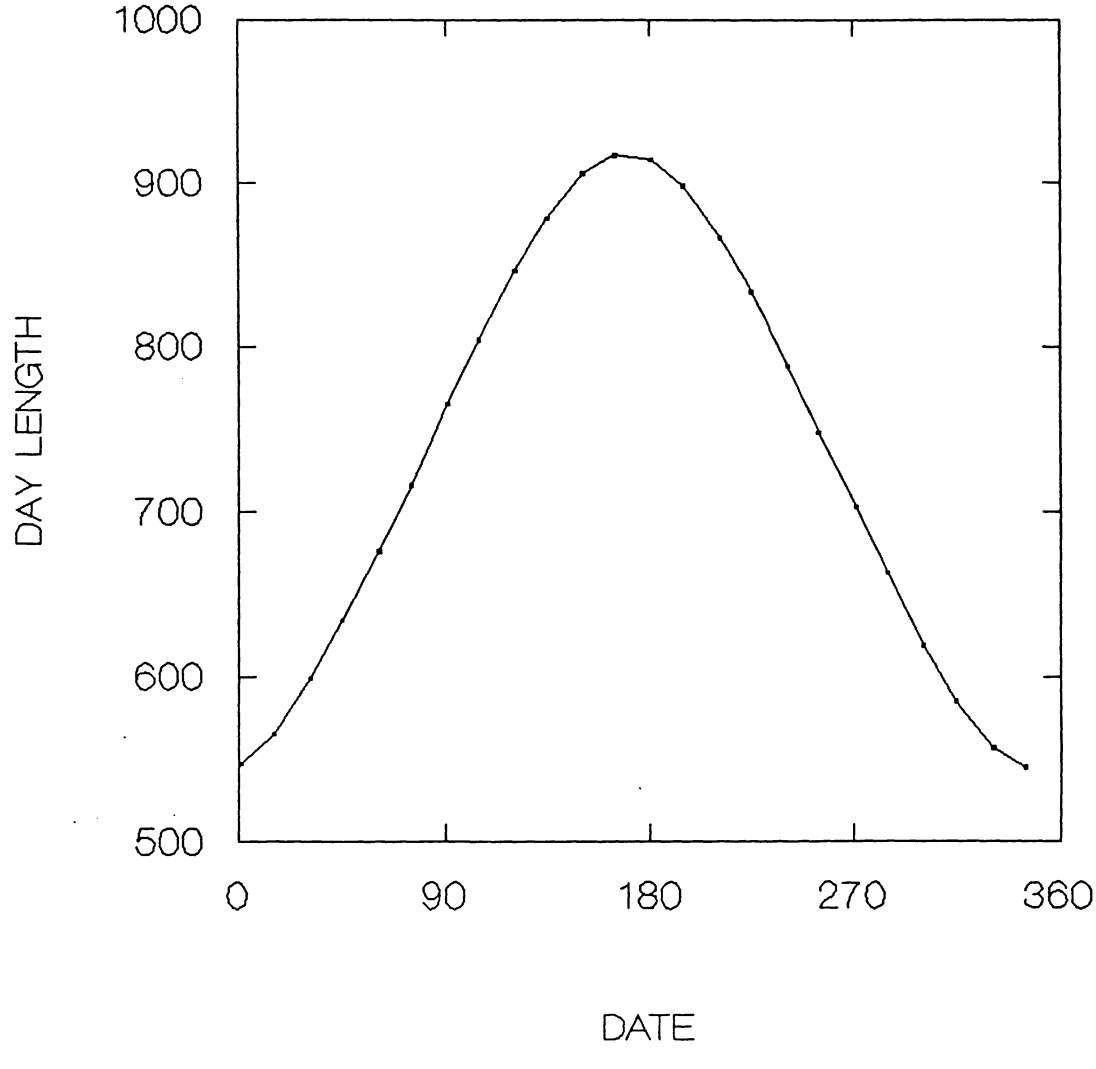
Figure 3. The optimal breeding seasons (nest-initiation through fledging) for birds with $n = 9$ and $w = 10$ indicated by shaded rectangle superimposed on a section of the annual cycle from Figure 1d. a) Optimal breeding season for birds with early food peak. b) Optimal breeding season for birds with late food peak. Note that cycles for day length and temperature are identical to those in a), but food distribution is shifted 30 days later.

Figure 4. Fitness of birds on 12 April vs. their fledging date. Open circles represent birds with 2 young, closed squares those with 5, and open triangles those with 8. Values for parental condition (w) of 3, 10, and 17 are plotted together, but notice that they do not even show up as different on this scale of resolution. a) Data for E group with early food peak. b) Data for L group with late food peak.

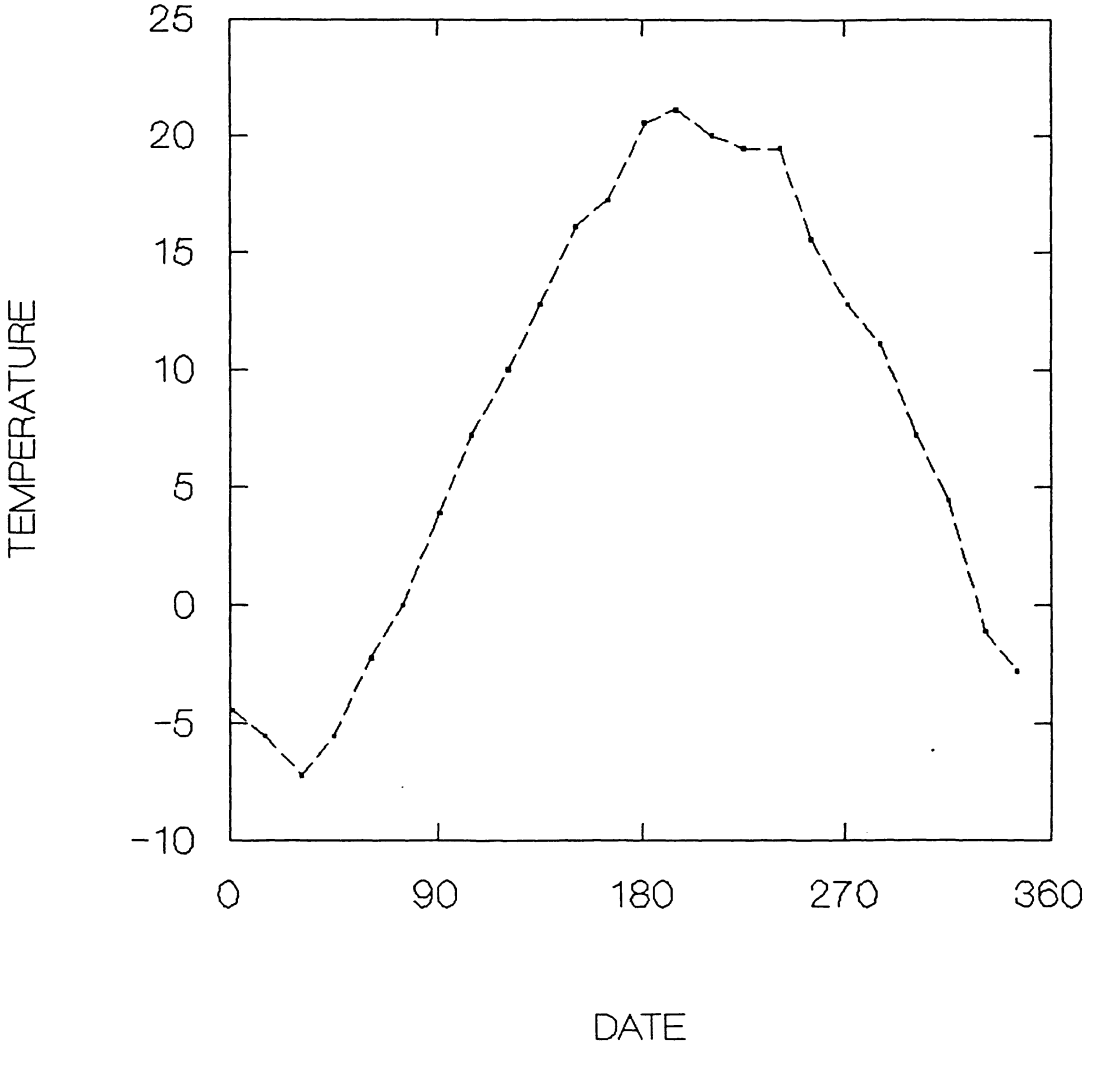
Figure 5. Optimal date of fledging offspring vs. brood size for E and L groups. These optima are determined by comparing fitnesses on a fixed calendar date (here March 25). The diamonds along the left margin represent the fledging dates compared for the E group and those along the right marging represent those compared for the L group.

Figure 6. Optimal date of fledging offspring vs. brood size for birds with early food peak. These optima are determined by comparing fitnesses a fixed number of days (in this case 55) in advance of the date of fledging.

Goutis and Wimmer Fig 1A



Gavis and Wimkler Fig. 1b



Goutis and Winkler Fig. 1C

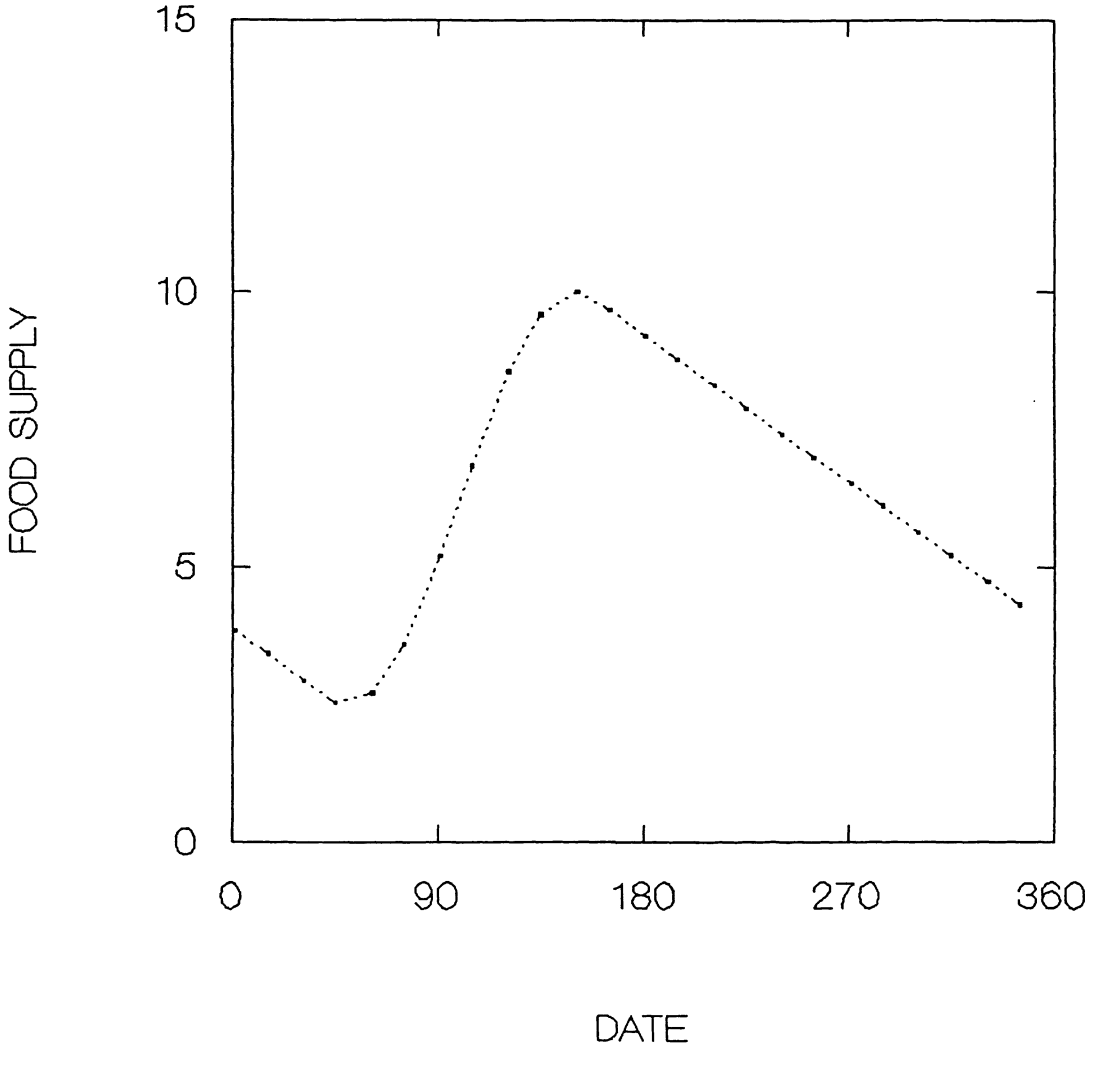
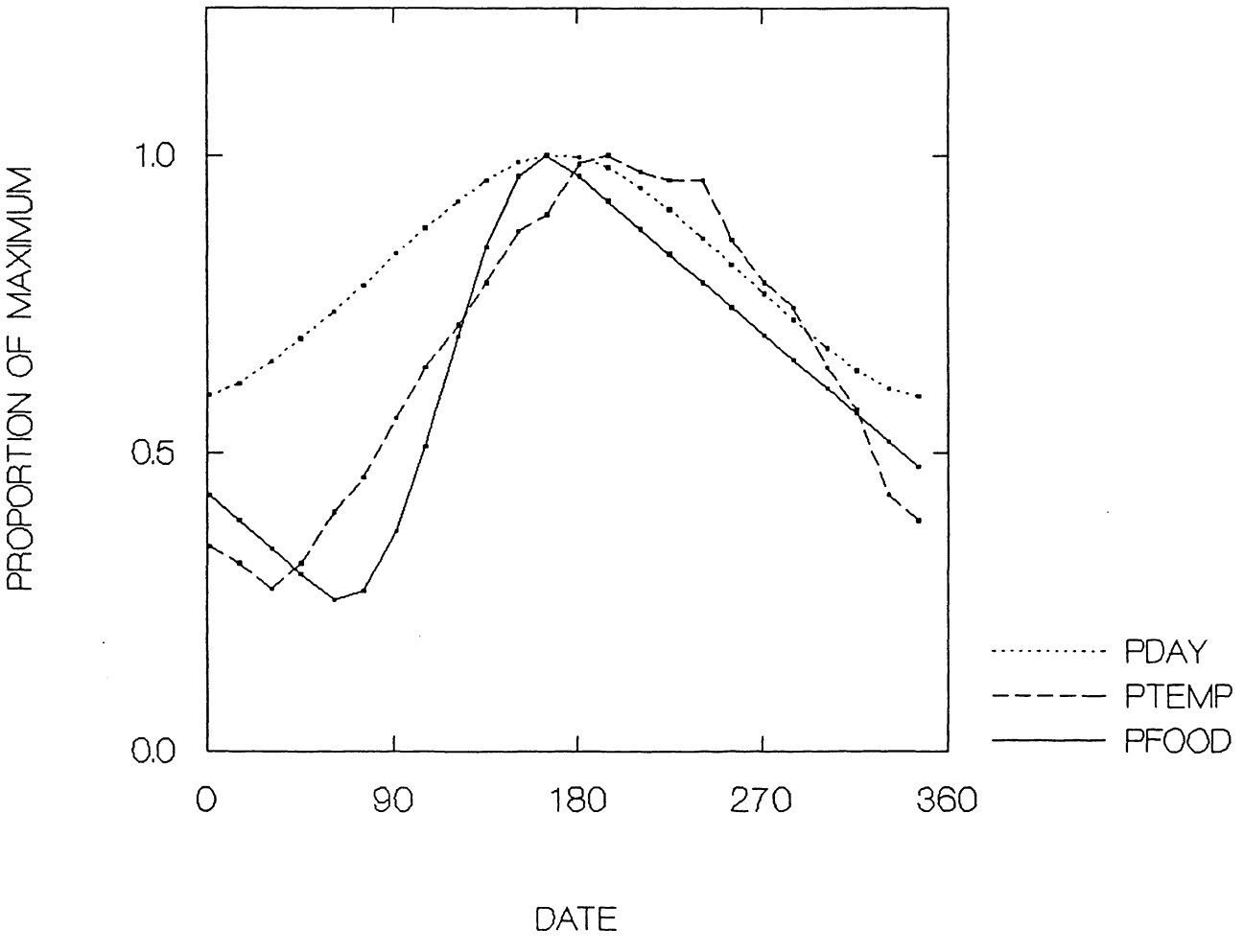


Fig 1d


PROPORTION OF MAXIMUM
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0.5
0.0
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90
180
270
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DATE
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PFOOD

Goulis and Mock Fig 2

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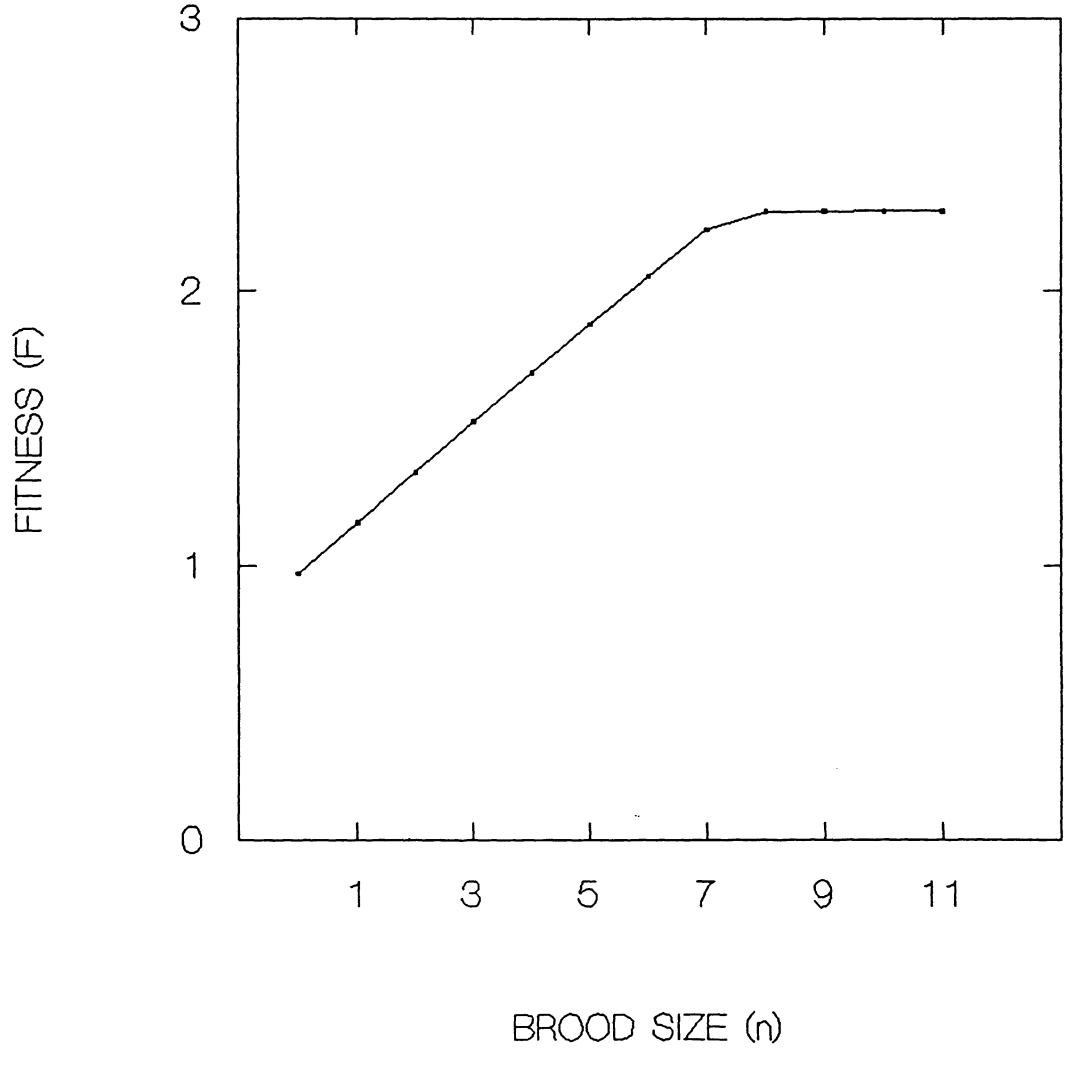
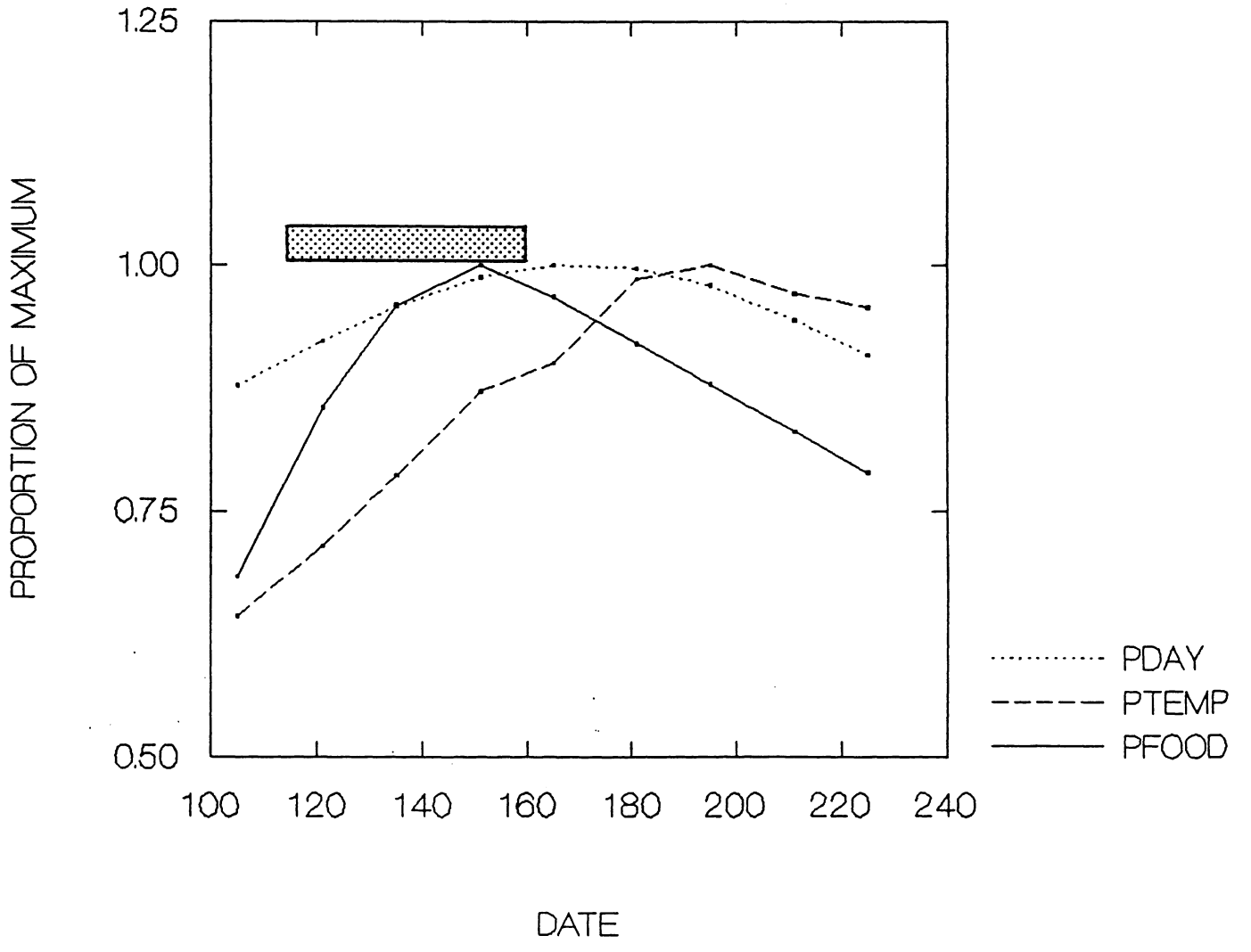
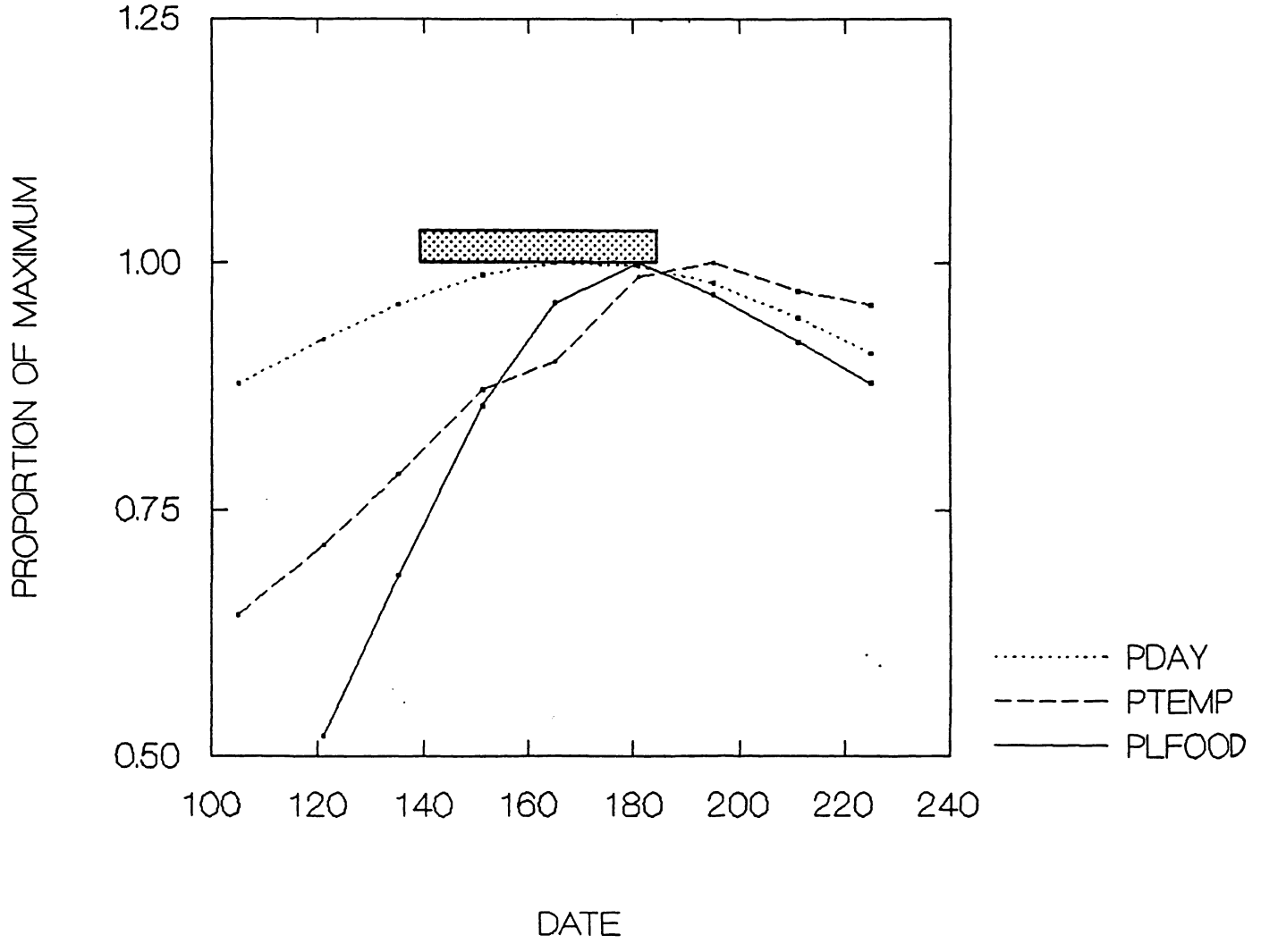


Gotthelf and Winkler Fig. 3A



Goutis and Winkler Fig. 3B



Goutis and Wilkler Fig 4A

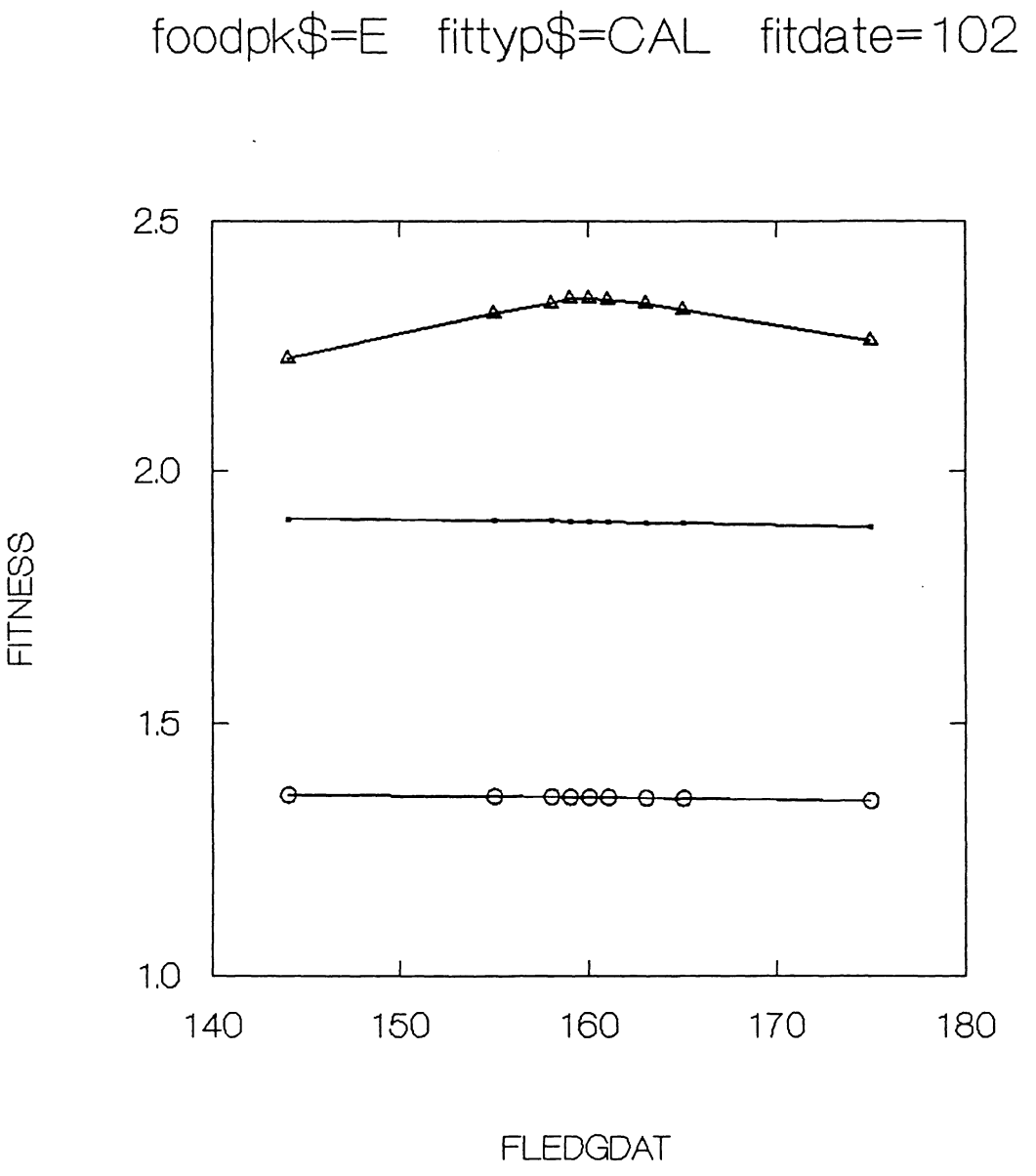
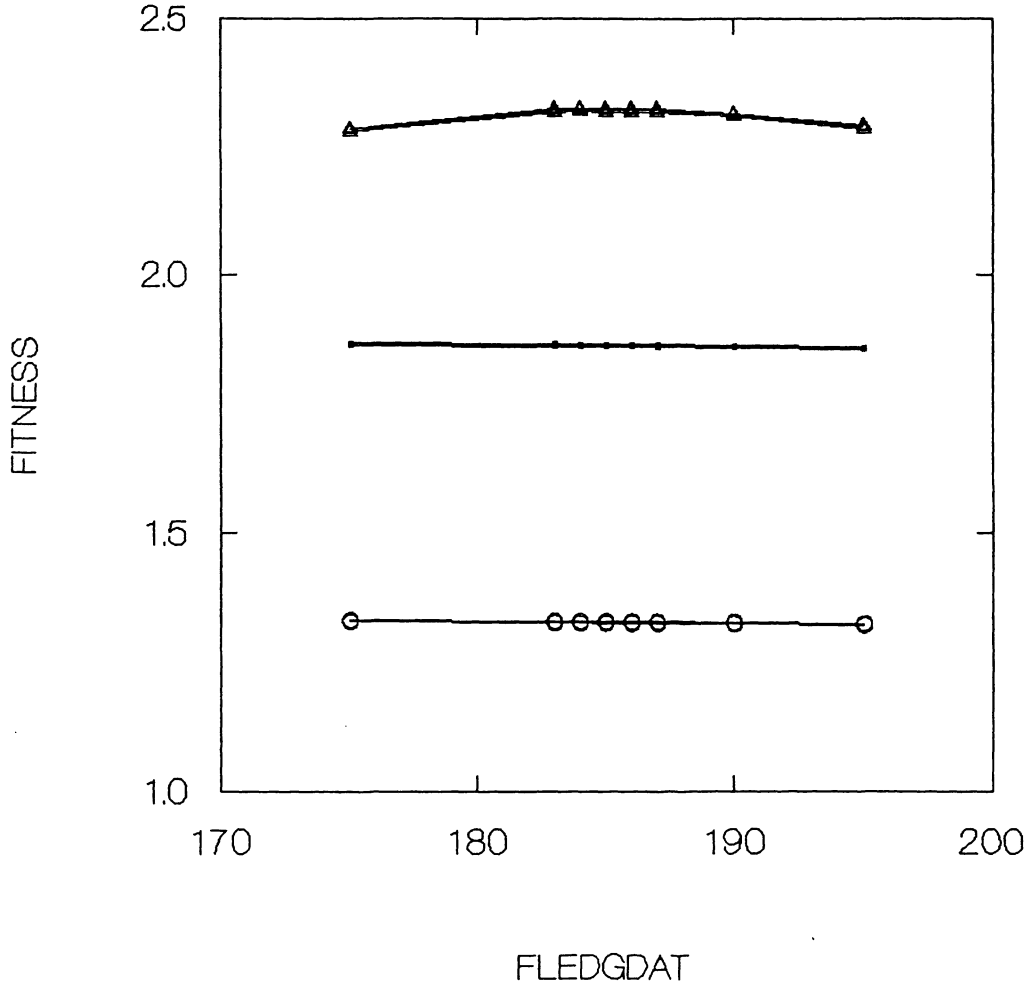
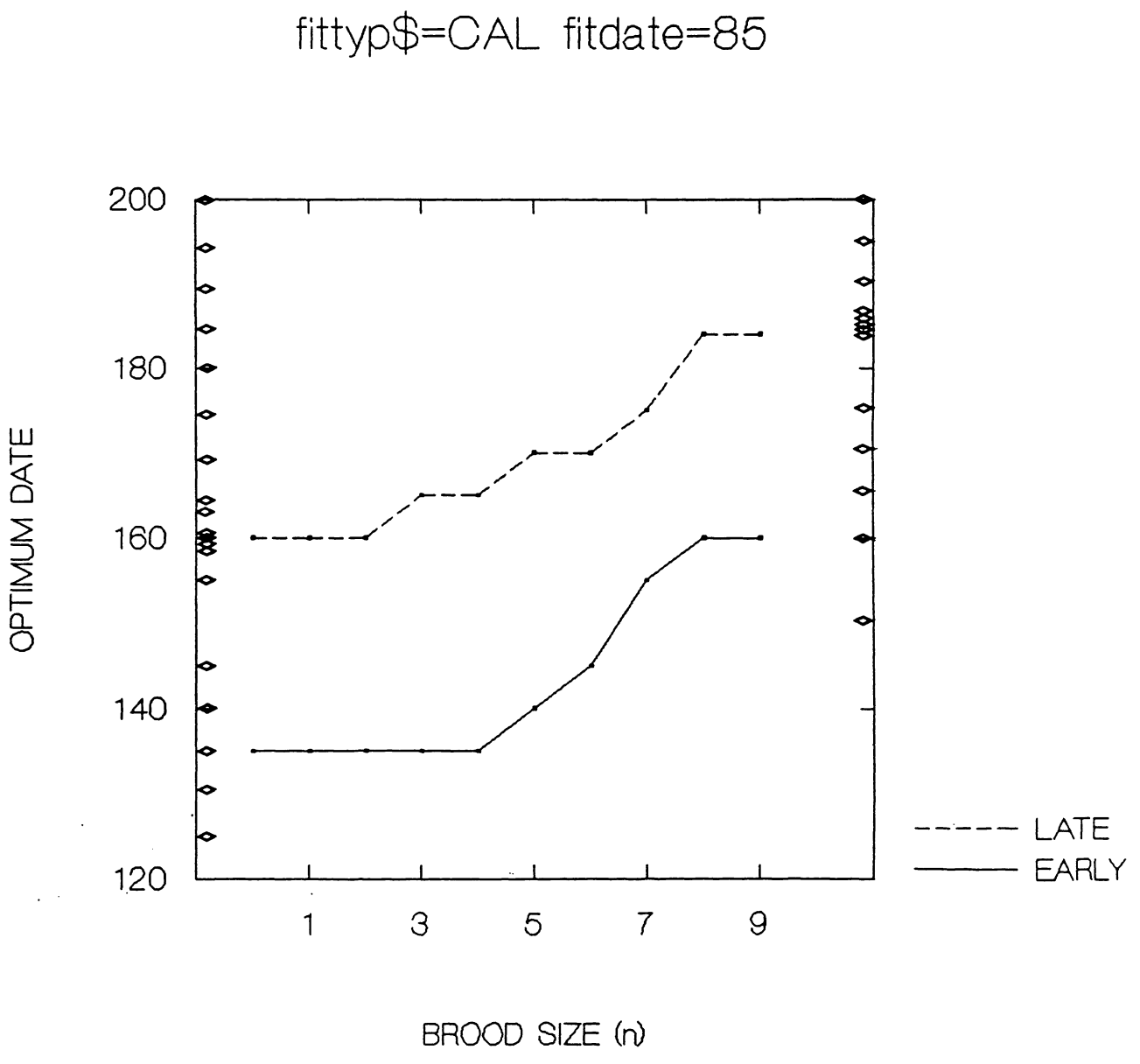


Fig 4B

foodpk$=L fittyp$=CAL fitdate=102



Goulis and Winkler Fig. 5



Gountis and Winkler Fig. 6